YIELD COMPONENT SELECTION IN WINTER WHEAT

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CHAPTER I

INTRODUCTION

An important objective in most wheat breeding programs is to increase the inherent yield potential of the wheat plant by genetic modification. Because of its low heritability, many problems are encountered in selecting for high yield potential in early generations following a cross. Breeders continue to search for better methods and techniques with which to improve the effectiveness of selection. It has been suggested that indirect selection for yield based on the components of yield, i.e. tiller number, kernels/spike, and kernel weight, might be more effective than direct selection for yield itself.

From the practical aspect, the most efficient selection method would make the least demands on time, land, and labor. Knowledge of the inheritance of yield components as well as the interrelationships among yield and the yield components are necessary if such a selection scheme is to be effective. When phenotypic and genetic correlations between yield and its components are partitioned into direct and indirect effects by path coefficient analyses, information is provided which could be useful to plant breeders in designing more effective plant breeding programs with regard to improved yield potential of wheat.

The objectives of this study were: (1) to examine the effective-ness of indirect selection based on yield components in terms of grain yield response, (2) to determine the interrelationships among yield and yield components and to determine the relative contribution of each component to grain yield by path analysis, and (3) to determine the realized heritability value for yield and each of the components of yield.

CHAPTER II

LITERATURE REVIEW

The theory and practice of selection in hybrid populations of self-pollinating crops have led to a general belief that a high efficiency of selection in early generations is possible only with highly heritable characters. Yield is a quantitative trait conditioned by many genes and is affected to a large extent by environmental influences. Consequently, selection for yield in early generations has not been generally effective. Fasoulas (8) suggested the honey-comb method of selection to minimize non-random environmental effects and to reduce bias due to non-additive genetic effects. This method, a type of stratified selection, was reported as being effective in selecting superior yielding genotypes from F_2 crosses of wheat (8). Nevertheless, selection for yield on a single-plant basis in early generations is not regarded as effective by most workers and hence selection for yield has usually been delayed until later generations (19). Even visual selection for yield among plots in replicated yield trials has not been effective in identifying high yielding lines of wheat (34). Various selection procedures have been suggested as a means of achieving high yielding genotypes of wheat. Among these, indirect selection based on yield components has been suggested as a procedure which should be more effective than selection based on yield *per se* (13, 22, 30, 36).

Yield component selection is a type of indirect selection which is based on various yield-related traits rather than selection based on yield _per se_. Grafius (11) had postulated a geometric concept of yield components in small grains and suggested that grain yield might be more effectively increased by selecting for one or more of the yield components. Grain yield in wheat is determined by three major components of yield: tiller number per plant or per unit area, the average number of kernels/spike, and the average kernel weight. When these components are measured without error and expressed in appropriate units, their product is total yield. Yield component selection for yield can be superior to direct selection when the component traits have higher heritability than the desired character, i.e. yield, and when the genetic correlation between the component and yield is high (7).

A search through the literature revealed very few reports on the effectiveness of yield component selection in small grains. Rasmusson and Cannell (25) found that selection for kernel weight was highly effective in increasing yield in barley crosses. In a study dealing with selection for yield potential in wheat, Sidwell (28) found that direct selection for yield was relatively ineffective whereas indirect selection based on kernel weight in the F_2 generation was more effective than direct selection for yield or indirect selection based on tiller number or kernels/spike. In his study involving a Sturdy X Centurk hard red winter wheat cross, the F_3 yield response to selection in F_2 for high kernel weight was much larger than that of selection for low kernel weight while the response of selection for high yield was only slightly better than that of selection for low yield. The F_3 yield response of selection for high tiller number and high number of kernels/spike were slightly smaller than that of selection for low tiller number and low kernels/spike. McNeal et al. (21) studied the response to selection based on yield and yield components for seven generations in a spring wheat cross (C.I. 13242 X Thatcher). By comparing the F_4 and F_8 means to the midparent value for each character, they found that indirect selection based on kernel weight and kernels/spike resulted in a significant increase in grain yield whereas selection based on yield and tiller number resulted in a significant decrease in yield. As a result of these findings they suggested that indirect selection based on kernel weight and kernels/spike should be considered as an effective procedure for yield improvement in wheat.

The effectiveness of yield component selection depends on the degree of heritability and the relationship of each of the yield components to yield. Heritability estimates, in turn, are dependent on the method of estimation used, the populations involved, and the unit of measurement as well as genetic and environmental influences (12). A number of heritability estimates have been reported in wheat. Chowdhry et al. (4) reported broad-sense heritability estimates of yield and yield components in five wheat crosses as follows: 0.36 to 0.63 for tiller number, 0.19 to 0.47 for kernels/spike, 0.19 to 0.67 for kernel weight, and 0.32 to 0.73 for grain yield. Several investigations at the Oklahoma Agricultural Experiment Station dealing with heritability estimates in wheat were summarized by Smith (30). In general, yield components had higher heritability coefficients than grain yield; and of the yield components, kernel weight tended to have the highest coefficient.

Alexander (2) conducted a genetic analysis on the three wheat populations that were utilized in this present study. The heritability estimates he obtained for kernel weight were high in one population (Aurora/Danne) and low in the other two populations (Aurora/Sage and Aurora/TAM W-101). The heritability estimates were intermediate in magnitude for tiller number and intermediate to low for kernels/spike. Low heritability estimates for grain yield were observed in all three populations.

The magnitude of heritability estimates for yield and yield components reported by Weibel (35), Kronstad and Foote (17), and Johnson et al. (14) in winter wheat were in agreement with those reported by Smith (30). Sharma and Knott (27), studying the inheritance of kernel weight in spring wheat, suggested the importance of kernel weight in terms of yield component selection since they found that this trait was controlled by as few as four genes. Selection based on kernel weight has been strongly recommended as a method for yield improvement by other workers (16, 26, 29).

Sidwell (28) calculated realized heritability coefficients in a winter wheat cross based on response in the F_3 due to selection in the F_2. He found that kernel weight had the highest realized heritability value. This was followed in descending order by kernels/spike, tiller number, and grain yield. McNeal et al. (21) studying yield and yield components in spring wheat found kernel weight to be the most heritable character and grain yield to be the least heritable.

Some knowledge of the interrelationships among various traits of the plant is necessary for planning an efficient selection program. The relationships of various agronomic characters with yield in wheat have been investigated by several workers. The results tended to indicate a high association of grain yield with one or more of its components although different components were important in different studies (9, 10, 15, 29). The phenotypic correlation between tiller number and grain yield was reported as positive and high in magnitude by Ketata et al. (15), Sidwell et al. (29), Drake (6) in winter wheat and McNeal (20) in spring wheat. This correlation was reported as positive and intermediate in magnitude by Fonseca and Patterson (9) and Thomas (33) in winter wheat. For kernels/spike, a high and positive correlation coefficient with yield was found by McNeal (20) in spring wheat, while a correlation of relatively low magnitude was reported by several workers in winter wheat (9, 29, 33). Most workers have reported a high to intermediate positive phenotypic correlation between kernel weight and grain yield (6, 9, 20, 29, 33), but a low correlation coefficient for this association was reported by Ketata et al. (15). The genetic correlation between yield and its components were found to be intermediate to low in magnitude by Sidwell et al. (29) and Ketata et al. (15).

Associations among the various yield components have been reported by several workers. The phenotypic interrelationships among yield components were all low but positive in a study reported by Drake (6). Negative correlations of intermediate magnitude between kernels/spike and kernel weight, and between kernels/spike and tiller number were found by Fonseca and Patterson (9). Phenotypic as well as genetic correlations between kernels/spike and the other two components were negative in a study conducted by Sidwell et al. (29) and similar results were reported for the correlations between kernel weight and the other yield components by Ketata et al. (15). The negative associations generally found among certain yield components was explained by Adams (1) as a result of competition for growth substances between genetically independent yield components.

To give an exact picture of the cause-and-effect relationships of each of the component characters toward grain yield, path coefficient analyses have been used to partition the correlation coefficients into direct and indirect effects. The path coefficient analysis often gives a somewhat different picture from that of simple correlation. This is due to the fact that the total correlation simply measures mutual association without regard to causation, whereas the path analysis specifies the causes and measures their relative importance (5). Therefore, the path coefficient analysis should provide a picture of the relative influence of different traits on yield. Phenotypic path analyses in a number of studies have shown that kernel weight exerted the greatest influence on yield in wheat (3, 9, 15, 29). Large direct effects on grain yield have been noted for tiller number, but studies on genetic path analyses in conjunction with phenotypic path analyses indicated that a large portion of that direct effect was probably due to nonadditive genetic or environmental effects or both (15, 29). Ketata et al. (15) also suggested the use of genetic correlations and genetic path coefficients for better interpretation since conclusions from correlation or path analysis based solely on phenotypic data may be misleading due to environmental influences.

This literature review, in general, indicates that indirect selection for yield should be more effective than direct selection for yield itself. As additional studies dealing with yield component selection in wheat are conducted, a more reliable picture of the effectiveness of this type of indirect selection will, no doubt, emerge.

CHAPTER III

MATERIALS AND METHODS

Breeding Populations

Three populations of winter wheat (Triticum aestivum L. em Thell.) were employed as the source of experimental material for this study. The populations, having one parent in common, were derived by crossing the U.S.S.R. cultivar 'Aurora' with the cultivars 'Sage' (Population 1), 'TAM W-101' (Population 2), and 'Danne' (Population 3). Sage, TAM W-101, and Danne are grown commercially in Oklahoma and Aurora is currently being used as a parent line in the Oklahoma breeding program. These four cultivars were chosen because of their contrasting characteristics with respect to yield component expression and other traits.

Aurora, an awnless cultivar grown widely in U.S.S.R., was developed at the Krasnodar Station, U.S.S.R., by crossing 'Lutescens-314h147' (Neuzucht X Bezostaya 4) with 'Bezostaya-1' followed by individual direct selection for productivity. It was released in 1971 (24). Under U.S. Southern Great Plains conditions, Aurora is intermediate in height and has relatively large spikes, large kernels, and a low tillering potential.

Sage was released by the Kansas Agricultural Experiment Station in 1973. It is a pure line selection from a backcross of Agent/4*-

Scout. Sage is midtall in plant height. It has a rather low kernel weight, few kernels/spike, and a high tillering potential (18).

TAM W-101 was released in 1971 by the Texas Agricultural Experiment Station. It was selected from the cross 'Norin 16/3/'Nebraska 60'//'Mediterranean'/'Hope'/4/'Bison'. TAM W-101 is a semi-dwarf type with high tillering potential, high kernel weight, and relatively few kernels/spike (23).

Danne was released by the Oklahoma Agricultural Experiment Station in 1970. It is a selection from a cross between 'Super Triumph' and C66-45-3, a strain of complex pedigree. The cross was made in 1950 by the late Joseph E. Danne, a private plant breeder. Danne is midtall in plant height. It has a rather low kernel weight, a high tillering potential, and relatively few kernels/spike (31).

The three populations were grown adjacent to each other but conducted as separate experiments at the Oklahoma Agricultural Experiment Station, Stillwater, during the 1975, 1976, and 1977 crop seasons, where they were studied respectively in the F_2, F_3, and F_4 generations.

Selection and Evaluation Procedures

In 1975, a total of 192 F_2 plants for each of the three populations was grown at the Stillwater Agronomy Research Station on a Bethany silt loam soil as a part of a genetic study by Alexander (2). In his study, the six generations (parental, F_1, F_2, BC_1, and BC_2) in each population were grown in a space-planted, randomized complete block design with four replications. Measurements were taken on all individual F_2 plants for tiller number, kernels/spike, kernel weight, and grain yield. These measurements were used as F_2 data sets for the present study and to identify appropriate F_2 plants for evaluation as F_3 progenies. Approximately 10% of the F_2 plants in each population were selected on the basis of high values for each of the characters mentioned above. Likewise, approximately 10% of the F_2 plants were selected on the basis of low values for these traits. There was some overlapping and certain F_2's were selected on the basis of more than one character. In each population, a total of 96 F_2 plants was selected on the basis of high and low values for yield and the three yield components. The F_3 progenies of these plants, referred to herein as F_3 lines, were studied in 1976. From the F_3 nurseries, a total of 48 progenies in each population was selected on the basis of high and low values for yield and the three yield components. These were studied in 1977 as F_4 progeny-progeny rows, referred to herein as F_4 lines.

The 96 F_3 lines were planted in single-row plots in a randomized complete block design with two replications. The rows were 1.33 m long and spaced 30 cm apart. The plots were solid-seeded at a rate of 100 seeds/row on a Norge loam soil with a tractor-mounted cone planter on October 19, 1975. Ammonium nitrate (NH_4NO_3) was applied as a preplant treatment at the rate of 38 kg per ha (34 lbs/A) on September 9, 1975, and also as a topdress treatment at the rate of 34 kg/ha (30 lbs/A) on February 20, 1976. Measurements for yield and yield components were made on each plot of the F_3 lines.

The 48 F_4 lines of each population were seeded on October 23, 1976, on a Bethany silt loam soil at the Stillwater Agronomy Research Station. The experimental design was a randomized complete block with four replications. Each single-row plot was 1.33 m long and rows were spaced 30 cm apart. Plots were seeded at a rate of 100 seeds/row by a tractor-mounted cone planter. A preplant treatment of ammonium phosphate (18-46-0) was applied at the rate of 112 kg/ha (100 lbs/A) on September 23, 1976. An ammonium nitrate topdressing at the rate of 38 kg/ha (34 lbs/A) was applied on February 24, 1977. Supplemental irrigation was applied on April 15, 1977.

Characters Evaluated

Tiller Number

In the F_2 generation, tiller number consisted of the number of seed-bearing tillers on each plant. In the F_3 and F_4 generations, tiller number was determined by counting the number of seed-bearing tillers in a random 30 cm section of each row.

Kernels/Spike

This was determined from three upper-story spikes on each F_2 plant. In the F_3 and F_4 generations, this trait was determined from six random upper-story spikes per row. In all three generations, the kernels obtained from the spike samples were counted and divided by the number of spikes to provide an average number of kernels per spike.

Kernel Weight

The kernel numbers and weights obtained from the spike samples mentioned above were used to calculate an average kernel weight value. This was expressed as grams per 1000 kernels.

Grain Yield

This trait was determined on the total weight in grams of the seed harvested from an individual plant in the F_2 generation and from a single-row plot in the F_3 and F_4 generations. In the F_3 and F_4 tests, rows were shortened to a 1 m length at harvest time to eliminate end-of-plot bias effects.

Statistical Analyses

In each population, the mean yield of F_3 and F_4 lines tracing to selected F_2 plants and the mean yield of F_4 lines tracing to selected F_3 lines were compared to determine the effectiveness of indirect selection for grain yield. There were three selection-response systems as follows: a) selection in F_2 with yield response in F_3, b) selection in F_2 with yield response in F_4, and c) selection in F_3 with yield response in F_4. There were eight selection groups, consisting of high and low groups for the four traits: tiller number, kernels/spike, kernel weight, and grain yield. Each selection group consisted of approximately 10 plants (in F_2) or 10 lines (in F_3).

In each of the three selection-response systems, the difference between the mean yield of the high selection group and that of the low selection group for each trait was determined. Statistical significance of these differences was tested by Duncan's multiple-range test (32), which utilized all the response data, including those of the non-selection group. Also, the effectiveness of yield component selection was studied by taking the 10 highest yielding lines of each population as measured in the F_4 test and examining their corresponding F_2 and F_3 selection group patterns.

Interrelationships among those characters studied were determined by computing phenotypic and genetic correlation coefficients among all possible pairs of variables. Phenotypic correlations were calculated using the variances and the covariances of the F_2 plants (192 plants/population) as:

$$r_p = \frac{\mathrm{Cov}(X,Y)F_2}{[\mathrm{Var}(X)F_2 \bullet \mathrm{Var}(Y)F_2]^{\frac{1}{2}}}$$

where $\mathrm{Cov}(X,Y)F_2$ represents the covariance between characters X and Y in the F_2 generation, and $\mathrm{Var}(X)F_2$ and $\mathrm{Var}(Y)F_2$ represent the variances of X and Y in the F_2, respectively.

Genetic correlations were computed using direct and indirect responses from the F_2-F_4 selection-response data as:

$$r_g = \left[\frac{CR_x \bullet CR_y}{R_x \bullet R_y}\right]^{\frac{1}{2}}$$

where selection group for character X in the F_2 generation was measured in the F_4 generation for character X as a direct response (R_x) and character Y as an indirect response (CR_y). Likewise, selection group for character Y was measured for direct response (R_y) and indirect response (CR_x). This is based on formulae given by Falconer (7).

The genetic correlation coefficients were adjusted to -1.0 or 1.0 when they fell outside these ranges. Tests for statistical significance of the phenotypic correlation coefficients are given but no such test is available for genetic correlations.

Both phenotypic and genetic correlations were further analyzed by a path-coefficient analysis as described by Dewey and Lu (5). This analysis measures the direct effect of one variable upon another and separates the correlation coefficients into components of direct and indirect effects. Path analysis requires a cause and effect directional assignment based on prior knowledge of the variables involved. Grain yield was considered as the resultant variable while tiller number, kernels/spike, and kernel weight were considered as the causal factors. Path coefficients were derived from the equation

$$Y = RP$$

where Y denotes the vector of correlation coefficients of yield and yield components. The symbol, R, represents a symmetric matrix whose elements are the correlation coefficients among yield components, while P is the vector of path coefficient.

In each of the three selection-response systems, a realized heritability was calculated for each character from an equation derived from Falconer (7). These equations will be discussed in more detail in the next chapter.

All statistical analyses were conducted at the Oklahoma State University Computer Center with assistance in programming by the Department of Statistics faculty.

CHAPTER IV

RESULTS AND DISCUSSION

Grain Yield Response from Yield Component Selection

The mean values of parents and selection groups for yield and yield components in the F_2 and F_3 tests of Populations 1, 2, and 3 are shown respectively in Tables I, II, and III. In Population 1 (Aurora/Sage), there were considerable differences between the two parents for all traits; with tiller number showing the greatest difference. In Population 2 (Aurora/TAM W-101), differences between the two parents were observed for all traits except kernel weight. Both parents had relatively high values for this trait. In Population 3 (Aurora/Danne), marked differences between the two parents were noted for tiller number and grain yield. Some differences, but to a lesser degree, were observed for kernels/spike and kernel weight. The parent, Aurora, in this population in the F_2 test was unaccountably low for kernel weight and grain yield.

The mean values for the selection groups in all three populations (Tables I, II, III) showed, as expected, that greater differences existed between high and low groups in the F_2 as compared to the F_3. The explanation for this is that selection groups were based on individual plants in the F_2 but on progeny rows in the F_3. The percent difference between the high and low selection groups ($\frac{H-L}{H}$ x 100) in the F_2 test ranged from 36.3% for kernel weight in Population 1 to 65.2% for grain yield in Population 3. In the F_3 test, differences ranged from 4.7% for tiller number in Population 2 to 30.2% for grain yield in Population 1. Most of the H-L differences in the F_3 were in the 8.0% to 10.0% class. For every trait, differences between high and low selection groups appeared to be of sufficient magnitude for effective indirect selection to be practiced.

The mean grain yield responses from high and low yield component selection in three types of selection-response systems (F_2-F_3, F_2-F_4, and F_3-F_4) are presented in Tables IV, V, and VI, respectively, for Populations 1, 2, and 3.

In Population 1, high selection for yield and the yield components resulted in a higher grain yield response than did low selection. For tiller number, kernel weight, and grain yield, these differences were statistically significant in all three selection-response systems. For kernels/spike, yield response differences were significant only in the F_2-F_3 selection-response system. Yield response differences were greater for selection based on kernel weight and grain yield than that based on tiller number or kernels/spike (Table IV).

In Population 2, grain yield response differences from high and low kernel weight selection were statistically significant in all three selection-response systems. Responses from selection based on grain yield were significant in two of three (F_2-F_3 and F_3-F_4) selection-response systems. For tiller number and kernels/spike, yield response differences were significant only in the F_3-F_4 selection-response system (Table V).

In Population 3, grain yield response differences from high and low selection based on grain yield itself were statistically significant in all three selection-response systems. Grain yield response differences from selection based on kernel weight were significant in two of three (F_2-F_3 and F_3-F_4) selection-response systems. For kernels/spike, yield response differences were significant only in the F_3-F_4 selection-response system. Yield response differences based on tiller number were not statistically significant in any of the three selection-response systems (Table VI).

Considering all three selection-response systems, it is evident in two out of three populations that an increase in grain yield would be expected if selection was made on the basis of kernel weight rather than on the basis of tiller number or kernels/spike. Also, selection based on yield itself appeared to be as effective as selection based on kernel weight. In general, these results tend to support the importance of indirect selection based on kernel weight as an effective procedure to increase grain yield in early generations. This is in agreement with previous studies by Sidwell (28) and McNeal et al. (21). Among the three populations, Population 2 (Aurora/TAM W-101) produced the highest average yield, suggesting that this would be the most promising population to continue in a breeding program in which yield improvement was the primary objective.

The apparent effectiveness of selection based on yield *per se* in early generations as indicated in Tables IV, V, and VI, is in disagreement with reports obtained by Sidwell (28) and McNeal et al. (21). This disagreement in the effectiveness of selection based on yield *per se* is probably due to populations studied and/or different selection procedures used. However, Fasoulas (8) has suggested that selection based on yield itself in early generations is an effective procedure for yield improvement in wheat.

The 10 highest yielding lines based on the F_4 test and their corresponding selection group patterns in the F_2 and F_3 generations for each of the three populations are shown in Table VII. A direct measure of the effectiveness of yield component selection for grain yield can be obtained from this table.

In Population 1, the high tiller number selection group would have identified three of the highest yielding lines in F_2 and four in the F_3. The high kernel weight selection group would have identified four of the highest yielding lines in F_2 and three in the F_3. The high yield selection group would have identified three of the highest yielding lines in the F_2 and five in the F_3. It is of interest to note that the highest yielding line in this population (No. 50048) was in the low tiller number selection group in both the F_2 and F_3 generations. This line was in the non-selection group for the other traits. Apparently its high yield came about from a favorable balance of the kernels/spike and kernel weight components. In Population 1, there was no definite pattern in the selection groups with regard to identifying the highest yielding lines.

In Population 2, the high yield selection group in both the F_2 and F_3 generations would have included five of the 10 highest yielding lines. This was the most effective selection group; it was followed by the high kernel weight selection group which would have included three lines in each generation of selection.

In Population 3, selection based on high kernel weight was the most effective. The high kernel weight selection group would have included five of the 10 highest yielding lines in both the F_2 and F_3 generations.

In all three populations, selection based on kernels/spike was the least effective method of selection for high grain yield.

These results indicate that the effectiveness of yield component selection may differ substantially in different populations. As shown in Table VII, selection based on kernel weight was most effective in Population 3 while selection based on yield itself was most effective in Population 2.

Correlation Among Characters

Phenotypic and genetic correlation coefficients among yield and yield components are presented in Tables VIII, IX, and X for Populations 1, 2, and 3, respectively. Phenotypic correlation coefficients were based on the F_2 generation (192 plants/population) while the genetic correlation coefficients were based on direct and indirect responses in the F_4 from selection in the F_2 generation as described in the previous chapter.

In Population 1 (Table VIII), grain yield had positive phenotypic correlation coefficients with tiller number, kernels/spike, and kernel weight, all of which were intermediate in magnitude. All three correlations were signfiicant at the 0.01 probability level. The phenotypic correlations among the yield components were all positive but low in magnitude. Kernel weight had the highest genetic correlation with grain yield (0.728) followed by tiller number (0.452) and kernels/spike (0.387). Among the yield components, the genetic correlation coefficient between tiller number and kernel weight was positive in sign and intermediate in magnitude (0.410). Negative genetic correlations were found between kernels/spike and tiller number (-0.422), and also between kernels/spike and kernel weight (-0.289).

In Population 2 (Table IX), the phenotypic correlation coefficients of yield with tiller number and kernel weight were of intermediate magnitude, while that of yield with kernels/spike was of low magnitude (0.300). All three of these correlations were positive in sign and significant at the 0.01 probability level. Grain yield had a positive genetic correlation with kernel weight of intermediate magnitude but had low genetic correlation coefficients with kernels/spike and tiller number. The genetic correlations among yield components were all negative. The genetic correlations between kernels/spike and kernel weight, between tiller number and kernel weight, and between tiller number and kernels/spike were respectively, -0.609, -0.371, and -0.053.

Phenotypic correlation coefficients between yield and the three components in Population 3 (Table X) were all positive, intermediate in magnitude and significant at the 0.01 probability level. The phenotypic correlations among the yield components were all positive, statistically significant but low in magnitude. A high negative association between tiller number and grain yield was found at the genetic level (-0.736). However, the genetic correlation between grain yield and kernel weight was positive in sign and intermediate in magnitude (0.684). A low coefficient was found for the genetic correlation between grain yield and kernels/spike. Among the yield components, kernel weight and tiller number had a positive genetic correlation coefficient of 0.433 while kernels/spike had a negative genetic correlation with both tiller number and kernel weight (-0.405 and -0.166, respectively).

Considering all three populations, grain yield had positive phenotypic correlation coefficients of intermediate magnitude with the three yield components. The phenotypic correlations among the yield components were generally of low magnitude. All were positive in sign with the exception of two comparisons (tiller number with kernels/spike and kernels/spike with kernel weight) in Population 2. A pattern was observed across all three populations for the genetic correlation of yield with kernel weight. Coefficients of this association were intermediate to high in magnitude and positive in all three populations. Also, the genetic correlation of kernels/spike with yield were positive but low in magnitude. The genetic correlations between tiller number and yield were not consistent either in sign or magnitude. The genetic correlations between kernels/spike and kernel weight were negative in all populations while low to intermediate genetic correlations were found between kernels/spike and tiller number.

The positive genetic associations between yield and kernel weight observed in all three populations were of sufficient magnitude to have important implications in a breeding program in which yield improvement is based on yield component selection. Also of interest was the presence of negative genetic correlations among some of the yield components. These negative relationships indicate that the yield components are not mutually independent, and that an increase in one could be accompanied by a decrease in another.

Path Coefficient Analyses

Path coefficient analysis requires the assignment of cause and effect relationships. In wheat, grain yield can be considered as the product of tiller number, kernels/spike, and kernel weight. Each of these three components influences grain yield by a direct contribution and also by acting in combination with the other two variables. Path analyses in this study were based on the phenotypic and genetic correlations as presented in the preceding section. Direct and indirect phenotypic and genetic effects of the yield components are summarized in Tables XI, XII, and XIII, respectively for Populations 1, 2, and 3. Path diagrams depicting these relationships are shown in Figures 1, 2, and 3. In the path diagrams, both phenotypic and genetic direct effects are measured by the path coefficient 'P', and the indirect effects among the yield components are measured by the correlation coefficient 'r'. The residual variable 'X' is assumed to be independent of the remaining variables and the square of 'X' measures the failure of the components to account for the total variation observed for grain yield.

In Population 1 (Table XI), the direct phenotypic effects for tiller number, kernels/spike, and kernel weight were 0.536, 0.421, and 0.330, respectively, and direct genetic effects of relatively high magnitude were observed for kernels/spike (0.811) and kernel weight (0.766). The direct genetic effect for tiller number was intermediate in magnitude (0.481). Indirect phenotypic effect as well as indirect genetic effects were of relatively low magnitude, indicating that indirect effects among the components had little net influence on yield.

The value of the direct effect can approach the total correlation value when a) both indirect effects are small or b) positive and negative values cancel out as was the case for genetic path analysis of yield vs tiller number in Population 1 (Table XI). However, sizable negative indirect effects between components could drastically reduce the net effect which would then be reflected in a total correlation lower than that for the direct effect as shown for the genetic path analysis of yield vs kernels/spike in Table XI.

The direct phenotypic effects in Population 2 (Table XII) are similar to those of Population 1, and as in the preceding case, the indirect effects were of little importance. The high positive direct genetic effect for kernel weight was 1.229 (values greater than 1.0 are possible since the path coefficient is a standardized partial-regression coefficient). Also, the direct genetic effect was high for kernels/spike, and intermediate in magnitude for tiller number. High to intermediate negative values were found in the indirect genetic effect of kernel weight via kernels/spike (-0.538), in the indirect effect of kernels/spike via kernel weight (-0.749), and in the indirect effect of tiller number via kernel weight (-0.456). The strong negative influence of such indirect effects gave total correlation values which were much lower than the direct effects of each variable (Table XII).

In Population 3 (Table XIII), the direct phenotypic effects were enhanced by indirect effects working in a positive direction so that the total correlation values exceeded the direct effect values. The direct phenotypic effects were all intermediate in magnitude with kernel weight having the highest value (0.443). A high negative direct genetic effect was observed for tiller number. Although the indirect effect of tiller number via kernel weight was positive and of intermediate magnitude, the total genetic correlation was still negative and high in magnitude (-0.736). The direct genetic effect for kernel weight was 1.235 but the total correlation was 0.684 because of the negative indirect effect via tiller number of -0.576.

The direct phenotypic effect of tiller number in Population 1 was slightly larger than that of the other two components while the direct genetic effects of kernels/spike and kernel weight were larger than that of tiller number (Figure 1). In Populations 2 and 3, kernel weight had the largest direct positive phenotypic and genetic effects (Figures 2 and 3).

Across all three populations, kernel weight had the greatest positive influence upon grain yield; therefore, selection for this character to improve grain yield would appear to be more effective than selection for tiller number or kernels/spike. Negative associations among the yield components could be a plausible explanation why the realized response in grain yield from indirect selection through kernel weight was lower than expected in two populations in this study. Nevertheless, these results are generally in agreement with reports by other workers (9, 15, 29).

Realized Heritability

According to Falconer (7), realized heritability is the ratio of response from selection to the selection differential ($h^2 = R/S$). The equation as further derived for the purpose of this study was:

$$h^2 = \frac{\bar{X}_{H(F_t)} - \bar{X}_{L(F_t)}}{\bar{X}_{H(F_{t-1})} - \bar{X}_{L(F_{t-1})}}$$

where $\bar{X}_H$ and $\bar{X}_L$ refer to the mean values of the high and low selection groups which are conditioned by F_t, the generation in which the response is measured, and F_{t-1}, the generation in which selection is applied.

There were three types of realized heritability coefficients corresponding to the three selection-response systems (or response-selection systems, in keeping with the way in which realized heritability calculations were made) discussed earlier in this chapter. For the convenience of the discussion, the realized heritability coefficients based on response in F_3 from selection in F_2 will be referred to as the realized heritability for F_3-F_2 or $h^2_{F_3-F_2}$, that based on response in F_4 from selection in F_2 will be referred to as $h^2_{F_4-F_2}$, and that based on response in F_4 from selection in F_3 will be referred to as $h^2_{F_4-F_3}$.

The realized heritability coefficients of yield and yield components for all three populations based on the three types of response-selection systems are shown in Table XIV. The realized heritability coefficients for F_3-F_2 and F_4-F_2 were low for tiller number, kernels/spike, and kernel weight in all populations. Unexpectedly, the realized heritability of grain yield based on F_3-F_2 and F_4-F_2 systems were high in Populations 1 and 3 and intermediate but still greater than those of the yield components in Population 2. These results of relatively high heritability values for yield are somewhat different from reports by other workers (14, 17, 21, 30, 35).

The realized heritability coefficients based on response in F_4 from selection in F_3 ($h^2_{F_4-F_3}$) should be more reliable than the other two types since the mean values of both the F_3 and F_4 generations were based on replicated plot averages while the F_2 values were based on single plant averages. Therefore, the following statements regarding realized heritability will be concerned with the $h^2_{F_4-F_3}$ coefficients only.

The realized heritability values for tiller number and grain yield were low in all populations. The realized heritability value for tiller number was slightly lower than that for grain yield in Populations 1 and 2 but slightly higher than that for grain yield in Population 3. In Populations 1 and 2, the realized heritability coefficients of kernels/ spike and kernel weight were intermediate in magnitude. They were high in Population 3. In all populations, kernel weight had the highest realized heritability coefficient when compared to other traits.

Based on response in F_4 from selection in F_3, kernels/spike and kernel weight were found to be more highly heritable with kernel weight having the highest realized heritability coefficient. This is in agreement with reports by McNeal et al. (21), Smith (30), and other (14, 17, 35).

The magnitude of $h^2_{F_4-F_3}$ realized heritability coefficients are consistent with the generally accepted picture regarding yield and yield components in wheat, viz: the expected heritabilities of these traits from low to high are grain yield, tiller number, kernels/spike, and kernel weight.

CHAPTER V

SUMMARY AND CONCLUSIONS

Three populations of winter wheat (Triticum aestivum L. em Thell.) derived by crossing the U.S.S.R. cultivar 'Aurora' in turn with the Hard Red Winter Wheat cultivars 'Sage', 'TAM W-101', and 'Danne' were studied in the F_2, F_3, and F_4 generations respectively during the 1975, 1976, and 1977 crop seasons at the Stillwater Agronomy Research Station. Characters studied in all generations were tiller number, kernels/spike, kernel weight, and grain yield.

In the F_2 generation, 192 spaced plants in each population were studied and the upper and lower 10% of the plants for the four traits were selected, resulting in 96 F_2 selected plants for each population. The F_3 progenies of these selected F_2 plants were grown in single-row plots in a randomized complete block design with two replications in 1976. Measurements for the four traits were made on each plot and the upper and lower 10% of the progenies (lines) in each population were selected, resulting in 48 progenies for each population. These 48 F_4 selected lines were grown in single-row plots in 1977 in a randomized complete block design with four replications. Measurements were made on each plot for yield and the three yield components in the F_4.

The effectiveness of yield component selection for each population was measured by examining three selection-response systems: selection in F_2 with yield response in F_3, selection in F_2 with yield response in

F_4, and selection in F_3 with yield response in F_4. Differences in grain yield between high and low selection groups based on tiller number, kernels/spike, kernel weight, and grain yield were examined. Considering all three selection-response systems, significant differences in yield between high and low selection groups were found for tiller number, kernel weight, and grain yield in Population 1 (Aurora/Sage), for kernel weight in Population 2 (Aurora/TAM W-101), and for grain yield in Population 3 (Aurora/Danne). These results indicate that selection based on kernel weight as well as that based on grain yield are more effective in increasing grain yield than selection based on tiller number or that based on kernels/spike.

A direct measure of the effectiveness of yield component selection was obtained by examining the F_2 and F_3 selection group patterns for each of the 10 highest yielding lines in each population based on F_4 performance. In general, results from this procedure indicated that there was no definite selection pattern in Population 1 while selection based on yield itself was most effective in Population 2 and selection based on kernel weight was most effective in Population 3. In all three populations, selection based on kernels/spike was the least effective method of selection for increasing grain yield.

Based on the results of this study, it can be concluded that indirect selection based on kernel weight would be an effective procedure to increase yield potential of wheat in early generations. This is in general agreement with other studies (21, 28). The apparent effectiveness of selection based on yield *per se* as found in this study is in disagreement with most of the previous studies reviewed. A possible explanation for this is that different populations and different procedures were involved. These results clearly indicate that the effectiveness of yield component selection is dependent on the particular populations studied and/or the particular selection procedures used. The highest yielding lines in this study were obtained from the cross between Aurora/TAM W-101 (Population 2), indicating that this would be the most promising population to continue in a breeding program for yield improvement.

Phenotypic correlations based on the F_2 data set showed that yield and the three yield components were positively associated, having correlation coefficients of intermediate magnitude. Positive genetic associations of intermediate to high magnitude were found between yield and kernel weight. The genetic correlations between yield and kernels/spike were also positive in sign but low in magnitude. The correlation coefficients between yield and tiller number were not consistent, either in sign or magnitude. Genetic correlations among the yield components showed that kernels/spike and kernel weight were negatively associated but this association was not strong. The same relationship was found for tiller number and kernels/spike.

The cause and effect relationships examined by path analysis indicated that the direct phenotypic effect of tiller number in Population 1 was slightly larger than that of the other two components while the direct genetic effects of kernels/spike and kernel weight were larger than that of tiller number. Kernel weight had the largest direct phenotypic and genetic effects in Populations 2 and 3.

In conclusion, considering all three populations, kernel weight had the greatest influence upon grain yield at both phenotypic and genetic levels. Therefore, selection based on kernel weight to improve grain yield would appear to be more effective than selection based on tiller number or kernels/spike. Negative genetic associations among certain yield components would indicate that these traits are not mutually independent, and that response levels in grain yield potential from yield component selection may be lower than projected.

Realized heritability values of yield and yield components were obtained from the ratio of response from selection to the selection differential on the basis of three response-selection systems: response in F_3 from selection in F_2, response in F_4 from selection in F_2, and response in F_4 from selection in F_3. The most useful estimates were based on the F_4-F_3 system undoubtedly because F_3 and F_4 values were based on replicated plot averages while the F_2 values were based on the average of individual plants. Realized heritability estimates, based on the F_4-F_3 response-selection system, showed that in all three populations, kernel weight had the highest heritability coefficient. Kernels/spike had the next highest value, while tiller number and grain yield had relatively low values. The high heritability value obtained for kernel weight reinforces the previous findings indicating the general effectiveness of increasing grain yield potential by indirect selection based on this trait.

TABLE I

MEAN VALUES FOR PARENTS AND SELECTION GROUPS FOR YIELD AND YIELD COMPONENTS IN F_2 AND F_3 OF POPULATION 1 (AURORA/SAGE)

Character Year Generation	Parents P_1 (Aurora)	 P_2 (Sage)	Selection Group* H	 L	 O	$\frac{H-L}{H} \times 100$ (%)
Tiller number						
1975 (F_2)	14.3	22.5	27.1	12.9	18.2	52.4
1976 (F_3)	34.0	48.8	42.1	37.9	38.8	9.9
Kernels/spike						
1975 (F_2)	55.5	46.8	62.3	35.9	48.4	42.4
1976 (F_3)	37.1	34.9	36.6	30.5	33.9	16.7
Kernel weight						
1975 (F_2)	32.6	28.6	42.4	27.0	34.9	36.3
1976 (F_3)	36.3	32.5	37.4	34.2	34.9	8.6
Grain yield						
1975 (F_2)	16.7	18.2	31.7	11.3	20.2	64.4
1976 (F_3)	83.9	95.4	93.7	65.4	85.5	30.2

*Mean values for high selection group (H), for low selection group (L), and for non-selection group (O).

TABLE II

MEAN VALUES FOR PARENTS AND SELECTION GROUPS FOR YIELD AND YIELD COMPONENTS IN F_2 AND F_3 OF POPULATION 2 (AURORA/TAM W-101)

Character / Year / Generation	Parents P_1 (Aurora)	Parents P_2 (TAM W-101)	Selection Group* H	Selection Group* L	Selection Group* O	$\frac{H-L}{H}$ x 100 (%)
Tiller number						
1975 (F_2)	15.9	25.1	28.7	14.5	20.5	49.5
1976 (F_3)	31.5	43.3	40.6	38.7	39.5	4.7
Kernels/spike						
1975 (F_2)	54.6	44.1	66.6	38.1	53.3	42.8
1976 (F_3)	42.2	32.5	35.7	32.4	34.9	9.2
Kernel weight						
1975 (F_2)	34.0	34.5	44.9	26.6	35.6	40.8
1976 (F_3)	39.2	40.1	40.2	36.4	37.6	9.5
Grain yield						
1975 (F_2)	16.7	18.2	36.3	14.5	24.3	60.1
1976 (F_3)	86.4	107.4	109.2	101.2	91.9	7.3

*Mean values for high selection group (H), for low selection group (L), and for non-selection group (O).

TABLE III

MEAN VALUES FOR PARENTS AND SELECTION GROUPS FOR YIELD AND YIELD COMPONENTS IN F_2 AND F_3 OF POPULATION 3 (AURORA/DANNE)

Character Year Generation	Parents P_1 (Aurora)	P_2 (Danne)	Selection Group* H	L	O	$\frac{H-L}{H}$ x 100 (%)
Tiller number						
1975 (F_2)	13.5	19.4	25.5	12.6	17.3	50.6
1976 (F_3)	25.8	36.3	31.4	28.6	30.4	8.9
Kernels/spike						
1975 (F_2)	53.3	48.8	63.4	36.9	49.1	41.8
1976 (F_3)	36.4	35.6	37.7	33.1	34.9	12.2
Kernel weight						
1975 (F_2)	26.3	29.7	39.4	22.8	30.3	42.1
1976 (F_3)	34.1	32.4	36.1	32.9	34.6	8.9
Grain yield						
1975 (F_2)	12.6	15.9	27.9	9.7	15.2	65.2
1976 (F_3)	62.2	80.5	77.4	60.9	71.6	21.3

*Mean values for high selection group (H), for low selection group (L), and for non-selection group (O).

TABLE IV

GRAIN YIELD RESPONSE FROM HIGH AND LOW YIELD COMPONENT SELECTION IN POPULATION 1 (AURORA/SAGE)

Character Selected	Selection-Response System	Selection Group High	Selection Group Low	Difference (High minus Low)
		Average Grain Yield (g/plot)		
Tiller number	F_2-F_3	83.3	76.1	7.2*
	F_2-F_4	100.6	94.7	5.9*
	F_3-F_4	108.5	93.6	14.9*
Kernels/spike	F_2-F_3	94.9	69.4	25.5*
	F_2-F_4	97.1	90.0	7.1
	F_3-F_4	100.3	87.7	12.6
Kernel weight	F_2-F_3	95.9	65.4	30.5*
	F_2-F_4	108.8	86.5	22.3*
	F_3-F_4	103.6	87.8	15.8*
Grain yield	F_2-F_3	93.7	65.4	28.3*
	F_2-F_4	101.4	84.5	16.9*
	F_3-F_4	108.4	85.6	22.8*

*Differences significant at the 5% level by Duncan's multiple-range test.

TABLE V

GRAIN YIELD RESPONSE FROM HIGH AND LOW YIELD COMPONENT SELECTION IN POPULATION 2 (AURORA/TAM W-101)

Character Selected	Selection-Response System	Selection Group High	Selection Group Low	Difference (High minus Low)
		Average Grain Yield (g/plot)		
Tiller number	F_2-F_3	96.5	95.8	0.7
	F_2-F_4	111.7	112.4	-0.7
	F_3-F_4	119.5	100.6	19.9*
Kernels/spike	F_2-F_3	95.6	92.4	3.2
	F_2-F_4	108.5	105.6	2.9
	F_3-F_4	113.1	103.8	9.3*
Kernel weight	F_2-F_3	100.0	89.9	10.1*
	F_2-F_4	114.7	103.6	11.1*
	F_3-F_4	117.9	95.2	22.7*
Grain yield	F_2-F_3	109.1	91.9	17.2*
	F_2-F_4	119.0	109.3	9.7
	F_3-F_4	125.6	99.7	25.9*

*Differences significant at the 5% level by Duncan's multiple-range test.

TABLE VI

GRAIN YIELD RESPONSE FROM HIGH AND LOW YIELD COMPONENT SELECTION IN POPULATION 3 (AURORA/DANNE)

Character Selected	Selection-Response System	Selection Group High	Selection Group Low	Difference (High minus Low)
		Average Grain Yield (g/plot)		
Tiller number	F_2-F_3	74.3	68.2	6.1
	F_2-F_4	106.5	98.4	8.1
	F_3-F_4	104.6	94.8	9.8
Kernels/spike	F_2-F_3	78.4	67.9	10.5
	F_2-F_4	103.5	102.2	1.3
	F_3-F_4	101.3	94.8	6.5*
Kernel weight	F_2-F_3	77.9	54.8	23.1*
	F_2-F_4	103.5	97.3	6.2
	F_3-F_4	107.2	93.3	13.9*
Grain yield	F_2-F_3	77.3	61.8	15.5*
	F_2-F_4	103.1	93.3	9.8*
	F_3-F_4	105.9	92.9	13.0*

*Differences significant at the 5% level by Duncan's multiple-range test.

TABLE VII

TEN HIGHEST YIELDING SUBPOPULATIONS IN F_4 AND CORRESPONDING SELECTION GROUP PATTERNS IN F_2 AND F_3

Entry No.	F_4 (Yield) (g/plot)	Seln. Group in F_2 TLN	K/S	KWT	YLD	Seln. Group in F_3 TLN	K/S	KWT	YLD[1]
POPN 1 (Aurora/Sage)									
50048	128.8	L	O	O	O	L	O	O	O
50028	122.2	O	O	O	H	H	L	O	O
50017	120.7	O	O	H	O	O	O	O	H
50022	118.9	O	O	H	O	H	O	H	H
50044	118.2	H	O	O	O	O	O	O	H
50037	117.0	H	O	H	H	O	O	O	H
50050	114.1	H	O	H	H	H	O	H	O
50041	111.9	L	O	O	O	O	O	H	O
50035	111.8	O	H	O	O	O	H	O	O
50004	111.3	O	H	O	O	H	O	O	H
	HIGH SELN GROUP TOTALS	3	2	4	3	4	1	3	5
POPN 2 (Aurora/TAM W-101)									
50203	138.5	O	H	O	H	H	O	O	H
50211	132.6	L	O	O	O	O	O	O	H
50206	129.1	O	L	H	L	O	L	O	O
50236	128.7	O	O	H	O	O	O	O	H
50245	127.6	H	H	O	H	H	O	O	H
50229	127.6	O	O	O	H	O	O	H	O
50214	125.7	O	O	O	H	H	O	O	O
50208	123.1	H	O	O	H	O	O	O	L
50205	121.9	O	L	H	O	O	O	H	H
50223	121.7	O	L	O	O	O	O	H	O
	HIGH SELN GROUP TOTALS	2	2	3	5	3	0	3	5
POPN 3 (Aurora/Danne)									
50413	128.5	H	H	H	O	H	L	O	O
50422	117.2	O	O	H	O	H	O	H	H
50438	116.8	H	O	H	O	O	O	O	H
50428	116.8	H	O	H	O	O	O	H	H
50403	112.3	O	O	L	O	L	O	O	O
50448	109.4	L	L	O	O	H	O	O	O
50414	108.4	H	O	H	H	O	O	H	O
50442	108.3	H	O	O	H	O	O	H	O
50410	107.8	L	O	O	O	O	O	H	O
50429	107.0	O	H	O	H	O	H	O	O
	HIGH SELN GROUP TOTALS	5	2	5	3	3	1	5	3

[1]TLN, K/S, KWT, and YLD, respectively, denote tiller number, kernels/spike, kernel weight, and grain yield.

TABLE VIII

PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN ALL POSSIBLE PAIRS OF CHARACTERS STUDIED IN POPULATION 1 (AURORA/SAGE)

Character	Tiller number	Kernels/spike	Kernel weight
Grain yield	0.650**[1]	0.549**	0.467**
	0.452	0.387	0.728
Tiller number		0.155*	0.148*
		-0.422	0.410
Kernels/spike			0.137
			-0.289

[1]The upper value is phenotypic correlation coefficient based on F_2 plants and the lower is genetic correlation coefficient based on the F_2-F_4 selection-response data.

For phenotypic correlations, * and ** denote significance at 0.05 and 0.01 probability level, respectively; tests for significance of genetic correlation are not available.

TABLE IX

PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN ALL POSSIBLE PAIRS OF CHARACTERS STUDIED IN POPULATION 2 (AURORA/TAM W-101)

Character	Tiller number	Kernels/spike	Kernel weight
Grain yield	0.591**[1]	0.300**	0.499**
	-0.083	0.114	0.535
Tiller number		-0.035	0.093
		-0.053	-0.371
Kernels/spike			-0.283
			-0.609

[1]The upper value is phenotypic correlation coefficient based on F_2 plants and the lower is genetic correlation coefficient based on the F_2-F_4 selection-response data.

For phenotypic correlations, ** denotes significance at 0.01 probability level; tests for significance of genetic correlation are not available.

TABLE X

PHENOTYPIC AND GENETIC CORRELATIONS BETWEEN ALL POSSIBLE PAIRS OF CHARACTERS STUDIED IN POPULATION 3 (AURORA/DANNE)

Character	Tiller number	Kernels/spike	Kernel weight
Grain yield	0.613**[1]	0.568**	0.633**
	-0.736	0.182	0.684
Tiller number		0.269**	0.235**
		-0.405	0.433
Kernels/spike			0.273**
			-0.166

[1]The upper value is phenotypic correlation coefficient based on F_2 plants and the lower is genetic correlation coefficient based on the F_2-F_4 selection-response data.

For phenotypic correlations, ** denotes significance at 0.01 probability level; tests for significance of genetic correlation are not available.

TABLE XI

PHENOTYPIC AND GENETIC PATH ANALYSES OF DIRECT AND INDIRECT EFFECTS OF YIELD COMPONENTS ON GRAIN YIELD IN POPULATION 1 (AURORA/SAGE)

Pathway	Value	
	Phenotypic	Genetic
Yield vs tiller number		
Direct effect	0.536	0.481
Indirect effect via kernel weight	0.049	0.314
Indirect effect via kernels/spike	0.065	-0.342
Total correlation	0.650	0.453
Yield vs kernels/spike		
Direct effect	0.421	0.811
Indirect effect via tiller number	0.083	-0.203
Indirect effect via kernel weight	0.045	-0.221
Total correlation	0.549	0.387
Yield vs kernel weight		
Direct effect	0.330	0.766
Indirect effect via tiller number	0.079	0.197
Indirect effect via kernels/spike	0.058	-0.235
Total correlation	0.467	0.728
Residual	0.515	0.308

TABLE XII

PHENOTYPIC AND GENETIC PATH ANALYSES OF DIRECT AND INDIRECT EFFECTS OF YIELD COMPONENTS ON GRAIN YIELD IN POPULATION 2 (AURORA/TAM W-101)

Pathway	Value	
	Phenotypic	Genetic
Yield vs tiller number		
Direct effect	0.552	0.419
Indirect effect via kernel weight	0.054	-0.456
Indirect effect via kernels/spike	-0.016	-0.046
Total correlation	0.590	-0.083
Yield vs kernels/spike		
Direct effect	0.486	0.885
Indirect effect via tiller number	-0.020	-0.022
Indirect effect via kernel weight	-0.166	-0.749
Total correlation	0.300	0.114
Yield vs kernel weight		
Direct effect	0.585	1.229
Indirect effect via tiller number	0.051	-0.156
Indirect effect via kernels/spike	-0.137	-0.538
Total correlation	0.499	0.535
Residual	0.487	0.455

TABLE XIII

PHENOTYPIC AND GENETIC PATH ANALYSES OF DIRECT AND INDIRECT EFFECTS OF YIELD COMPONENTS ON GRAIN YIELD IN POPULATION 3 (AURORA/DANNE)

Pathway	Value	
	Phenotypic	Genetic
Yield vs tiller number		
Direct effect	0.419	-1.332
Indirect effect via kernel weight	0.090	0.535
Indirect effect via kernels/spike	0.104	0.061
Total correlation	0.613	-0.736
Yield vs kernels/spike		
Direct effect	0.334	-0.152
Indirect effect via tiller number	0.113	0.539
Indirect effect via kernel weight	0.121	-0.205
Total correlation	0.568	0.182
Yield vs kernel weight		
Direct effect	0.443	1.235
Indirect effect via tiller number	0.099	-0.576
Indirect effect via kernels/spike	0.091	0.025
Total correlation	0.633	0.684
Residual	0.522	1.341

TABLE XIV

REALIZED HERITABILITY FOR YIELD AND YIELD COMPONENTS

Character	Response-selection generations	POPN 1[1]	POPN 2	POPN 3
Tiller number	$h^2_{F_3-F_2}$	0.294[2]	0.134	0.218
	$h^2_{F_4-F_2}$	0.252	0.290	0.397
	$h^2_{F_4-F_3}$	0.248	0.155	0.335
Kernels/spike	$h^2_{F_3-F_2}$	0.230	0.116	0.172
	$h^2_{F_4-F_2}$	0.241	0.212	0.298
	$h^2_{F_4-F_3}$	0.478	0.588	0.722
Kernel weight	$h^2_{F_3-F_2}$	0.213	0.207	0.191
	$h^2_{F_4-F_2}$	0.295	0.114	0.079
	$h^2_{F_4-F_3}$	0.501	0.667	0.861
Grain yield	$h^2_{F_3-F_2}$	0.407	0.376	0.847
	$h^2_{F_4-F_2}$	0.816	0.459	0.525
	$h^2_{F_4-F_3}$	0.316	0.385	0.251

[1]Populations 1, 2, and 3 are respectively Aurora/Sage, Aurora/TAM W-101, and Aurora/Danne.

[2]The upper, middle, and lower values are respectively based on response of one character in F_3 from high and low selection of that character in F_2; likewise response in F_4 from selection in F_2, and response in F_4 from selection in F_3.

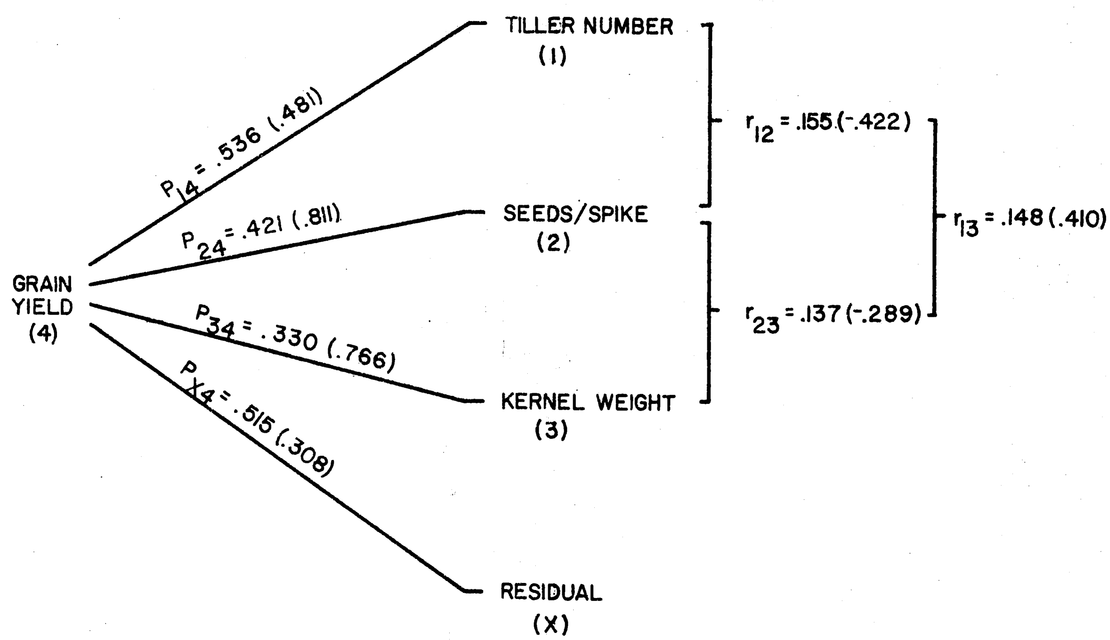

Figure 1. Path Diagram of Direct and Indirect Influences of Yield Components on Yield in Population 1 (Aurora/Sage).

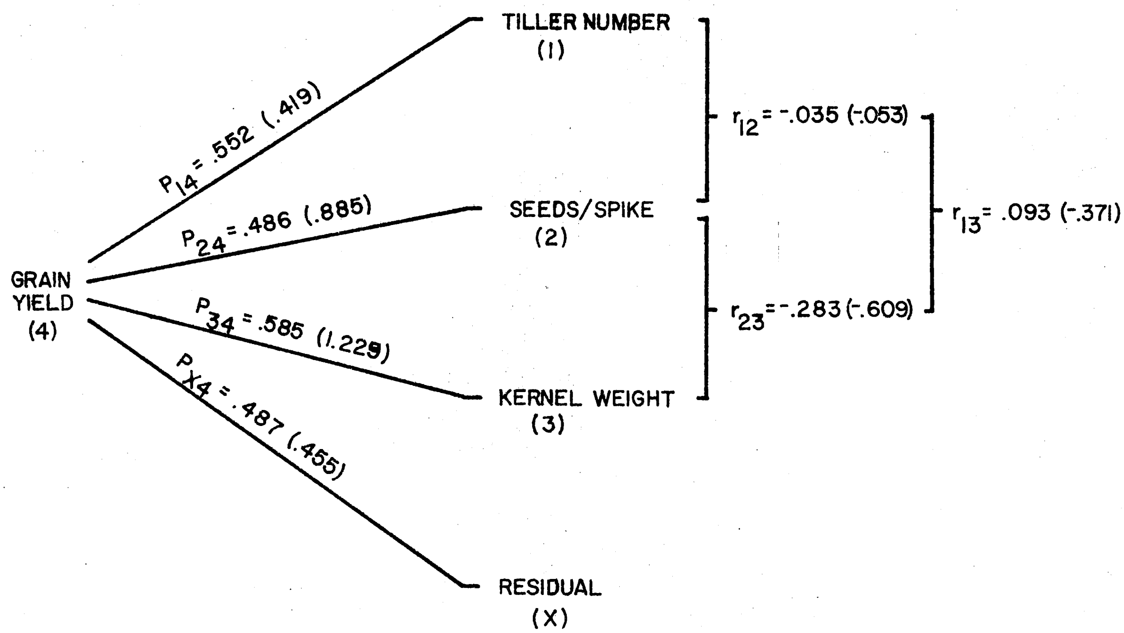

Figure 2. Path Diagram of Direct and Indirect Influences of Yield Components on Yield in Population 2 (Aurora/TAM W-101).

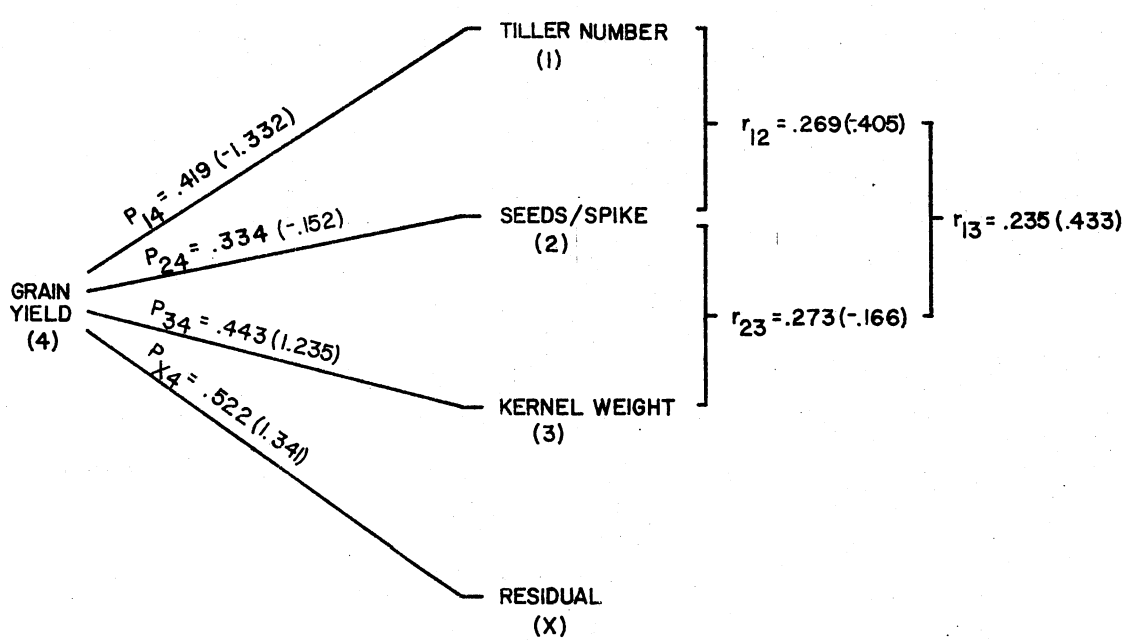

Figure 3. Path Diagram of Direct and Indirect Influences of Yield Components on Yield in Population 3 (Aurora/Danne).

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